A PROPOSAL FOR CLASSIFICATION OF THE ANNUAL SPECIES OF STEPHANOMERIA (COMPOSITAE)

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Among the most common and conspicuous plants of the late-summer flora in many regions of California and adjacent areas are the annual species of *Stephanomeria* (Cichorieae, Compositae). These plants, some of which tower more than eight feet high, are readily identifiable to genus, even when observed from a car zooming along at 60 m.p.h., but their morphological intergradation has vexed many collectors who have attempted to key them to species.

Recent extensive field study and experimental analysis, however, have elucidated the characteristics of the individual species and have clarified their relationships. As a group, the annual Stephanomerias comprise both a polyploid complex and a homogamic complex (Grant, 1953) in which both tetraploid and diploid taxa are morphologically intermediate between two divergent diploid species, *Stephanomeria exigua* and *S. virgata,* both of which are polytypic. Experimental evidence regarding the evolutionary relationships of *S. exigua, S. virgata,* and *S. diegensis,* a morphologically intermediate diploid species, has been presented elsewhere (Gottlieb, 1971). The purpose of this paper is to propose a taxonomic arrangement of all the annual species and to present a key for their identification. *Stephanomeria* also includes about nine or ten herbaceous perennial species, some of which are widely distributed in western North America, that are clearly distinct from the annual species in habit and morphology. Their relationships have not been investigated and they are not discussed in this report.

The taxonomic difficulties in the annual Stephanomerias result from their substantial morphological similarities. Thus, Ferris (1960) noted, "Different strains are sometimes locally recognizable but intergrading forms are constantly to be found even in the same region." With the exception of absence of grooves on the achenes, which is now known to distinguish *S. virgata,* no single morphological key character is restricted to a single taxon. Species identification is further complicated by the overlap in geographical ranges, particularly in central and southern California. In addition, what has proven to be one of the most serviceable characters for identification, the state of the calyculate involucral bracts (reflexed or appressed to the involucre), is not easy to ascertain on pressed herbarium specimens. Many of the characters that have been utilized in various recent keys for *Stephanomeria* such as pappus color, achene shape and surface condition, and stem width are misleading because of their genetic variability and phenotypic plasticity. In this group of plants, the species and their morphological limits became apparent only following cytological examination of numerous populations and the

results of experimental hybridizations. These studies (Gottlieb, 1969, 1971) revealed the widespread occurrence of tetraploid populations, the karyotypic differences among the diploid species, and the type and strength of reproductive isolating barriers among the species.

The most divergent species are the widespread diploids, *S. exigua* and *S. virgata,* that differ in many morphological features, karyotype, and chromosomal structural arrangement resulting in strong reduction of the fertility of hybrids between them. Although the differences between the species apparently mark a fundamental phylogenetic divergence, their features are combined in several other species, in slightly different combinations in each case. These morphologically intermediate taxa plus the occurrence of hybrid swarms or hybrid individuals where different Stephanomerias grow together in nature effectively blur the morphological distinctions between *S. exigua* and *S. virgata,* and are responsible for the taxonomic complexities of the entire group.

For example, all the morphological features of the diploid *Stephanomeria diegensis,* with the exception of high floret number and long lateral pinnae along the pappus bristles, are an amalgam of those found in *S. exigua* and *S. virgata* ssp. *virgata.* Similarly, the allotetraploid *Stephanomeria elata* is morphologically intermediate between *S. exigua* and *S. virgata* but with a different combination of characters. To a lesser extent, both *S. exigua* ssp. *carotifera* and *S. exigua* ssp. *macrocarpa* have morphological features (reflexed calyculate bracts and certain features of the pappus in subspecies *carotifera*) that are also found in *S. virgata* ssp. *virgata.* A reasonable hypothesis to explain the morphological intermediacy of these taxa that has not been overthrown by the available evidence is that they have resulted from independent interspecific hybridizations between *S. exigua* and *S. virgata* followed by selection for genotypes with a new balance of adaptation (Gottlieb, 1971, unpublished).

In order to deal with this complex situation, the species concept adopted in *Stephanomeria* utilizes both experimental results and convenience. The decision to recognize *S. exigua* and *S. virgata* as polytypic species rather than recognizing a number of separate species is based on relative degrees of reproductive isolation as well as morphological and chromosomal differentiation. The differences between any pair of subspecies of *S. exigua,* or between the two subspecies of *S. virgata,* are substantially less well developed than are the differences between the two species or between either of them and *S. diegensis.* Biologically, the taxa recognized within each species have reached the level of divergence designated semispecies, and their biological relationships seem best depicted by treating them taxonomically as subspecies rather than species.

Stephanomeria paniculata is diploid, self-compatible, and highly self-pollinating in the greenhouse (Gottlieb, 1969). It has the same karyotype as *S. exigua,* and its morphological features also ally it to that species, particularly subspecies *coronaria.* Substantial reproductive isolation is present since experimental hybrids between *S. paniculata* and subspecies

coronaria are difficult to obtain and when they are produced average less than 25% pollen stainability (Gottlieb, 1969). Since the subspecies that comprise *S. exigua* are moderately to strongly divergent and, since on the basis of its morphological features, *S. paniculata* is most likely derived from the self-incompatible *S. exigua* ssp. *coronaria,* one could argue that it too should be treated taxonomically as another subspecies of *S. exigua.* Although this would not be inconsistent with what is known of the biology of these organisms, nothing would be gained by such a taxonomy. In a complex group of plants like *Stephanomeria* that is actively differentiating, and in which morphological distinctions are few and bridged by intermediate taxa, the designation of taxonomic rank is arbitrary. *Stephanomeria paniculata* has been recognized as a species for more than 100 years and, probably, because of its northern distribution (fig. 1), has not been confused with the other taxa of *Stephanomeria.* To reduce it to subspecific rank does not further clarify its relationships. Therefore, I propose that it is not necessary to change the taxonomic rank of *S. paniculata.*

Stephanomeria diegensis is more sharply isolated reproductively from both *S. exigua* and *S. virgata* than they are from each other, yet its morphological characteristics are a composite of their features. These three species can be considered a homogamic complex. The particular combination of features that distinguish *S. diegensis* is present in all its populations and, together with its striking reproductive isolation, warrant its recognition as a species.

Stephanomeria elata comprises all the annual tetraploid populations of *Stephanomeria.* These are a highly variable group of populations that cytogenetical analyses reveal have an allotetraploid origin between *S. exigua* and *S. virgata* (Gottlieb, 1969). The three species together are a classic example of a polyploid complex. The tetraploid populations exhibit substantial interpopulation morphological variability, but the pattern of their features together with geographical distribution generally permits their identification without counting chromosomes. Triploid hybrids between *S. elata* and *S. virgata* are known in nature, but no evidence is available that such individuals serve to transfer genes between ploidy levels. The tetraploid plants are self-compatible and, since they are highly self-pollinated (at least in the greenhouse), it has not been possible to make hybrids among them. Since the tetraploid populations are considered to have a common origin and in the absence of positive evidence of any reproductive isolation among them, it is convenient to treat them as a single species. However, the present treatment may have to be modified when additional information is amassed.

Taxonomy

The morphological descriptions presented below emphasize characters that are useful in differentiating the taxa and ignore certain features that are alike in all of them. All have taproots and form basal leaf rosettes

before the single erect stem is produced. All have leaves or leafy bracts on the stem and branches; the leaves vary from entire to pinnatifid and are oblanceolate to spatulate in shape. The involucres are cylindrical or oblong with a series of equal-sized phyllaries equivalent in number to the number of florets and subtended by fewer calyculate bracts. The ligules are generally similar in length (9–15 mm) and width (2.8–4.7 mm) except that those of the self-compatible *S. exigua* ssp. *macrocarpa, S. paniculata,* and *S. elata* are smaller. The achenes are light tan to dark brown, oblong, sometimes curved, truncate at the apex, five-ribbed, with the surface between the ribs either smooth or rugose-tuberculate. Measurements presented in the key and in the descriptions below are averages for populations. Representative specimens from my collections will be distributed to UC, RSA, SBBG, MICH, DAV, and NY. Only some of the specimens examined are cited below. Included are collections that document distributions and some that are widely distributed in herbaria for reference purposes. Collection numbers prefixed by *G* are my own.

Key to the Annual Taxa of Stephanomeria

Achenes grooved longitudinally.

Heads in small panicles along branches; peduncles 10–40 mm long.

Calyculate bracts strongly reflexed; South Coast Ranges of California . . . . . 1c. *S. exigua* ssp. *carotifera*

Calyculate bracts appressed.

Peduncles and involucres glabrous or sparsely glandular; Mojave Desert and east to Texas. 1a. *S. exigua* ssp. *exigua*

Peduncles and involucres conspicuously glandular; coastal mountains and valleys from Los Angeles to northern Baja California. 1b. *S. exigua* ssp. *deanei*

Heads solitary or clustered on short divaricate peduncles $<$ 10 mm long.

Pappus bristles not thickened at base, free, breaking off cleanly from achene.

Pappus bristles plumose on upper 80–85% of length; pubescence on involucres glandular; coastal southern California to northern Baja California. 3. *S. diegensis*

Pappus bristles plumose throughout; pubescence glandular or not; widely distributed, southwestern Oregon south to Santa Barbara and western slope Sierra Nevada . . . . . 4. *S. elata*

Pappus bristles at least slightly thickened, often connate in groups of 2–4 at bases, breaking off above bases which remain adnate to achene.

Achenes averaging > 5.5 mm long; western slope Sierra Nevada . . . 1d. *S. exigua* ssp. *macrocarpa*

Achenes < 4.5 mm long.

Calyculate bracts appressed.

Pappus bristles plumose throughout with heavily thickened, setulose bases; achenes averaging > 3.5 mm long; northern California and Great Basin. 2. *S. paniculata*

Pappus bristles plumose on upper 60–85% of length, connate or not; achenes averaging < 3.5 mm long; widely distributed California and north in Great Basin. 1e. *S. exigua* ssp. *coronaria*

Calyculate bracts reflexed . . . . . 4. *S. elata*

Achenes not grooved.

Calyculate bracts reflexed; 8–9 florets per head; southern California. 5a. *S. virgata* ssp. *virgata*

Calyculate bracts appressed; 5–6 florets per head; widely distributed from southwestern Oregon in both Coast Ranges and Sierra Nevada to northern Baja California. 5b. *S. virgata* ssp. *pleurocarpa*

1a. Stephanomeria exigua Nutt. ssp. exigua, Trans. Amer. Phil. Soc. 2:7:428. 1841.

Stephanomeria pentachaeta D.C. Eaton, Bot. King Expl. 199. 1871.

(Type from "Truckee and Humboldt Valleys", Nevada, illustrated in above)

Ptiloria exigua Greene, Pittonia 2:132. 1890.

Ptiloria pentachaeta Greene, Pittonia 2:133. 1890.

Stephanomeria exigua var. *pentachaeta* Hall, Univ. Calif. Publ. Bot. 3:260. 1907.

Peduncles and involucres glabrous or sparsely glandular–pubescent; heads paniculate, peduncles 10–40 mm long (fig. 2); heads average 5–8 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink on upper surface, purple-tinged on back; achenes averaging 2.6–3.2 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 5–13 in number, plumose on the upper 45–55% of their length, thickened and often connate in groups of 2–4 at the bases which generally remain adnate to the achene (when only 5 bristles are present, these break off cleanly). $\mathbf{n = 8}$.

Type. "Colorado of the west, 1834–35", T. Nuttall. (Holotype: GH!)

Distribution. Widely distributed (fig. 1) from Mojave and Colorado Deserts in California across the southwest to western Colorado and west-

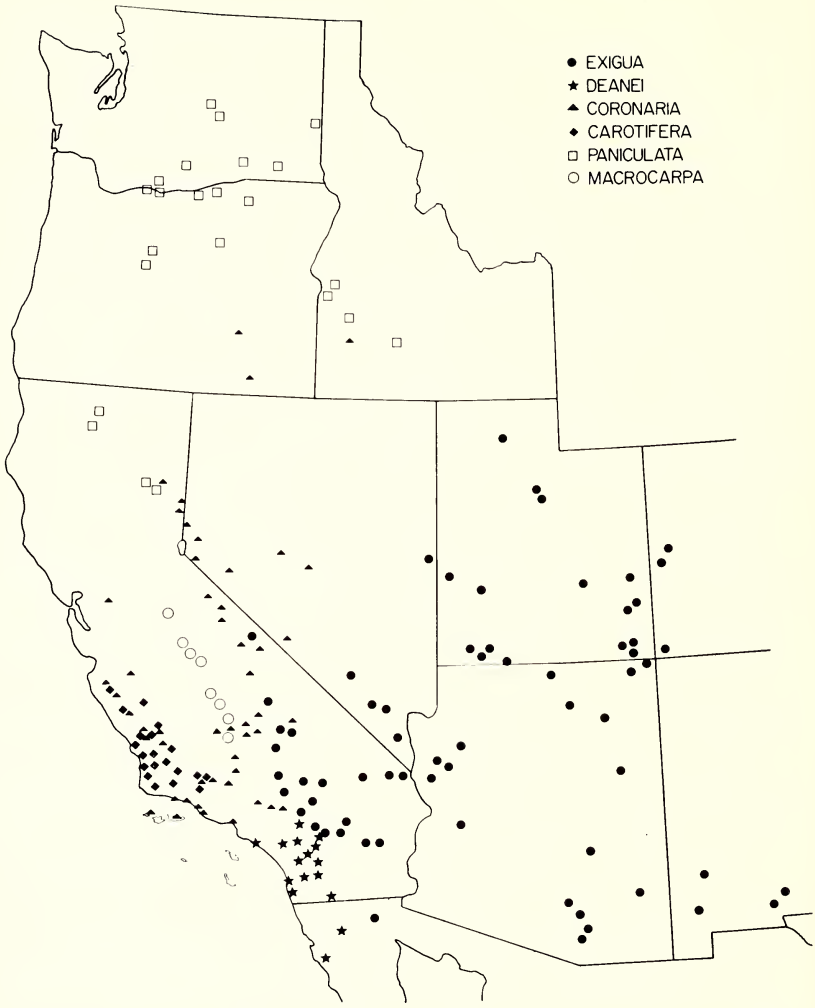

Fig. 1. Distribution of the five subspecies of *Stephanomeria exigua* and of *S. paniculata*.

ern Texas. In sandy soil in sagebrush, creosote bush, and *Coleogyne* shrub communities. Flowers May to July.

Representative specimens. TEXAS. El Paso Co.: lower slopes of Franklin Mt., east side, bajada at end of mountain road, *Correll and Correll 38619*. NEW MEXICO. Dona Ana Co.: 1 mile west of Organ on U.S. 70 and south ½ mile on Blair Canyon Road. *G-684*. Hidalgo Co.: Lordsburg, *Eastwood 8545*. Luna Co.: 1 mile west of Road 81 on U.S. 10, *G-686*. ARIZONA. Apache Co.: Canyon de Chelly National Monument, south rim, across from Antelope Point, *Bailey 375;* Junction to Petrified Forest, east of Holbrook, *Raven 13020*. Coconino Co.: 14 miles north-

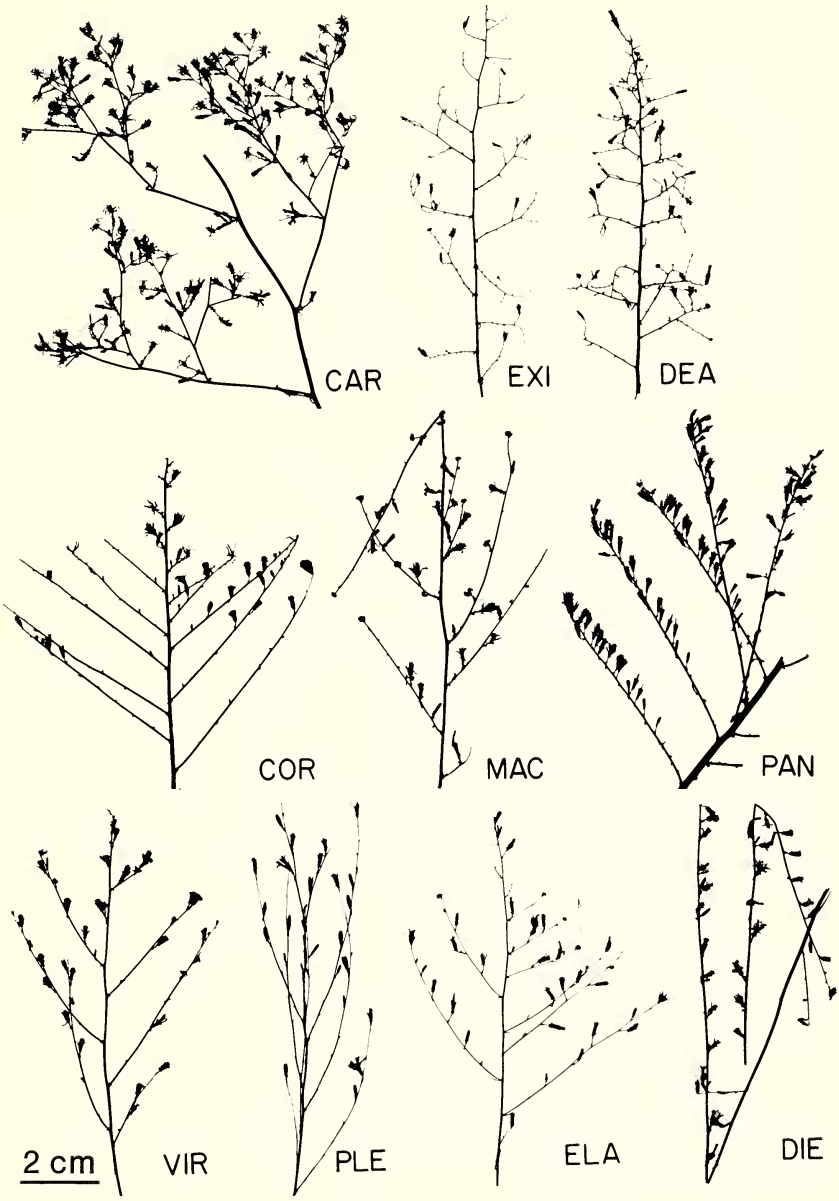

FIG. 2. Silhouettes of the branches of the annual taxa of *Stephanomeria* (modified with additions after Gottlieb, 1971, fig. 5).

east of Tuba City, *Cronquist 9140;* Middle Mesa, *Gould and Phillips 4738.* Mohave Co.: Vulcan's Throne, Toroweap, *Cottam 13357;* between Hualpai Wash and junction of Pierce's Ferry Road with U.S. 466, *Ferris 9889;* Yucca, *Jones 3931.* Navajo

Co.: Monument Valley, *Eastwood and Howell 6654*. Pima Co.: Santa Rita Experimental Range, Study Area 199B, *G-6811*. Yuma Co.: Harcuvar Mountains, *Peebles 13876*. COLORADO. Mesa Co.: Grand Junction, *Eastwood 7218*. UTAH. Milford, *Jones 1798*. Grand Co.: ½ mile north of Arches National Monument on U.S. 160, *G-691*. Kane Co.: East entrance Zion National Park, *Kamb 633;* 1 mile east of Kanab, *Maguire 18902*. San Juan Co.: Rainbow Bridge Trail, *J. T. Howell 24653*. Utah Co.: Springville, *Jones 5618*. NEVADA. Clark Co.: Kyle Canyon, *Clokey 7764;* 12 miles north of Searchlight at Marshall's Wash, *Gullion 323*. Lander Co.: Toiyabe Range, *Eastwood and Howell 7354*. Nye Co.: 4–6 miles north of Tonopah on road to Cloverdale, *Henning 185*. White Pine Co.: 2 miles south of Baker, Snake Range, *Maguire 20850*. CALIFORNIA. Inyo Co.: Olancha, *Hall and Chandler 7344*. Kern Co.: Red Rock Canyon, *Twisselmann 15411*. Mono Co.: Chalfant Flats, Shealy, *Duran 3487*. Riverside Co.: Hot Springs, 8 miles north of Garnet, *Rose 35675*. San Bernardino Co.: Palm Springs, *Eastwood 2961;* Adelanto, *Parish 11814;* Deadman's Point, *J. T. Howell 2504;* 21 miles east of Lucerne Valley on Old Womman Springs Road, *G-6650*.

Pappus bristle number is variable in *Stephanomeria exigua*. Those plants with a pappus of five bristles, *Stephanomeria pentachaeta,* are not distinct from subspecies *exigua;* individuals with five bristles appear occasionally in populations throughout the distribution and are fully interfertile with plants having higher bristle numbers.

1b. **Stephanomeria exigua** ssp. **deanei** (MacBride) n. comb.

Stephanomeria exigua var. *deanei* MacBride, Contrib. Gray Herb., n.s., 53:22. 1918.

Ptiloria exigua var. *deanei* MacBride ex. Davids. & Moxley. Fl. S. Calif. 355. 1923.

Peduncles and involucres conspicuously glandular-pubescent; heads paniculate, peduncles 10–40 mm long (fig. 2); heads averaging 7–9 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 2.1–2.4 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 9-14 in number, plumose on the upper 55–60% of their length, thickened and generally connate in groups of 2–4 at the bases which usually remain adnate to the achene when the bristles break off. **n = 8.**

Type. "California, San Diego Co., Sweetwater Valley, Las Paderas Ranch, 23 July 1888, G. C. Deane." (Holotype: GH!)

Distribution. Sandy fields and chaparral in coastal mountains and valleys from Los Angeles County south to northern Baja California (fig. 1). Flowers June to October.

Representative specimens. CALIFORNIA. Riverside Co.: Chalk Hill, San Jacinto Mountains, *Hall 7*. San Diego Co.: Julian, Oct. 16, 1894, *T. S. Brandegee;* Lakeside, *Hall 7439;* 1.8 miles from Ballena on road to Ramona, *Raven and Snow 9585;* 1 mile west of Manzanita, at Tierra del Sol turnoff from U.S. 80, *G-6635;* between Anza and Cahuilla on Rt. 71, *G-6658;* Rincon Springs, *G-66160*. MEXICO. Baja California: Cardon Grande, April 23, 1889, *T. S. Brandegee;* El Llano de Santana, May 10, 1889, *T. S. Brandegee;* San Carlos River, *Eastwood 12422;* Las Animas

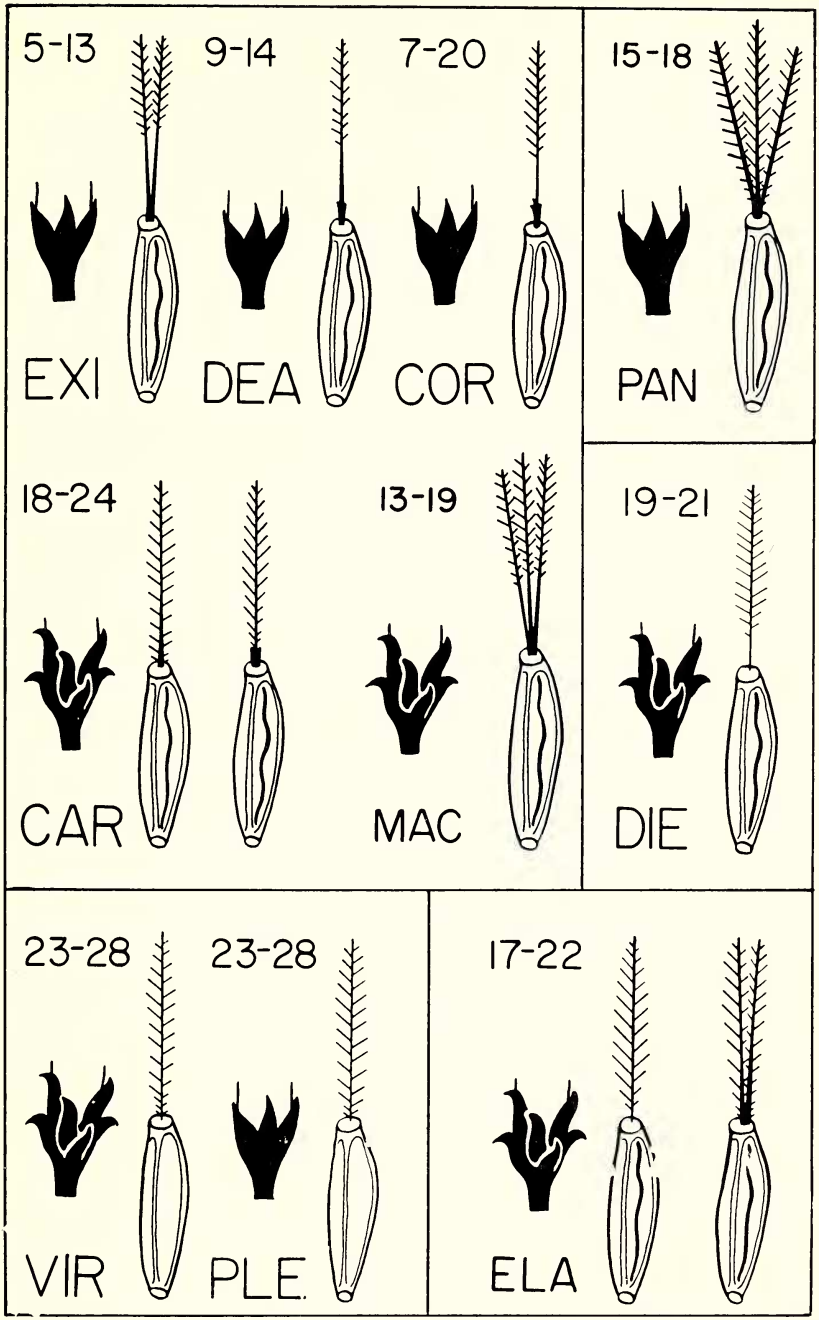

FIG. 3. Diagram of the morphological characteristics of the achenes, pappus bristles including number per achene, and involucres of the annual taxa of *Stephanomeria* (modified with additions after Gottlieb, 1971, fig. 4).

Canyon, 23 miles south of Ensenada, *Wiggins and Demaree 4712;* Yellow Pine Belt between Ojos Negros and Neji Ranch, *Wiggins and Gillespie 4136.*

Subspecies *deanei* is most closely allied to subspecies *exigua*. The two are separated on the basis of a few constant morphological characters, their allopatric distribution, and a reduction in fertility of hybrids between them.

1c. **Stephanomeria exigua** ssp. **carotifera** (Hoover) n. comb.
Stephanomeria carotifera Hoover, Leafl. W. Bot. 10:252. 1966.

Herbage glabrous or tomentose on stems and involucres; heads paniculate, peduncles averaging greater than 12 mm long (fig. 2); heads averaging 7–9 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 3.2–4.3 mm long, five-sided with a narrow longitudinal groove on each side; pappus bristles either thickened or not (fig. 3), when thickened, often connate at the bases in groups of 2–4, bristles plumose to the top of the thickening, and breaking off above the bases that remain adnate to the achene, when not thickened, distinct at the base, bristles plumose their entire length, and breaking off completely or nearly so; in both types, bristles average 18–24 in number. **n = 8.**

Type. "Open south-facing hill near San Bernardo Creek east of Morro Bay, in clay among serpentine rock, July 11, 1964, Hoover 9191." (Holotype: CAS 453,631!)

Distribution. Inland populations in open, sandy and shale soils in inner South Coast Ranges (fig. 1) such as the Temblor and Diablo Ranges and north into various creeks draining into the Salinas and San Antonio Valleys, or coastal populations on sand dunes and shale and serpentine from the vicinity of San Luis Obispo to Surf, Santa Barbara County, and on Figueroa Mountain, Santa Barbara County, Hi Mountain, San Luis Obispo County, and Sespe Creek, Ventura County. Flowers August to October.

Representative specimens. CALIFORNIA. Kern Co.: Santos Canyon, 10 miles south of Blackwell's Corner, *Twisselmann 832;* Mt. Abel Road, 5.1 miles north of Maricopa Highway, *Twisselmann 3135;* ½ mile east of Temblor Mountain summit on Route 58, *G-6845.* Monterey Co.: 15 miles west of Greenfield on Jamesburg Road, *J. T. Howell 27477;* Mustang Grade, between Mustang summit and San Lorenzo Creek, *J. T. Howell 40073;* 1 mile south of Jolon on Jolon-Lockwood Road, *G-66127.* San Luis Obispo Co.: Palo Prieta Canyon near summit, *Twisselmann 3108;* Twisselmann Ranch, summit of Choice Valley, *Twisselmann 5564;* Carrisa Plains School, *Twisselmann 7915;* Bellevue-Santa Fe School, *Hoover 9977;* Grover City, *Hoover 10092;* Oso Flaco Lake, *Hoover 10865;* 3 miles northeast of Tepusquest Road on Colson Canyon Road, *G-7072;* near summit of Hi Mountain, south of Pozo, *G-7076;* 6.5 miles west of Shandon on Route 41, *G-7080.* Santa Barbara Co.: dunes at Surf, *Pollard, July 22, 1954;* 7 miles west of Buellton on Route 150, *Pollard, September 13, 1956;* Union Oil Refinery, Route 1, west of Santa Maria, *G-7074;* immediately east of Figueroa Mountain Campground on Cachuma Saddle Road, *G-7134.* Ventura Co.: Quatal Canyon, *Twisselmann 2319;* 2–3 miles south of Sandstone Campground, Sespe Creek, *G-7064.*

Subspecies *carotifera* was originally described as a species because it was thought to be perennial and morphologically distinct from other perennial Stephanomerias. However, field and greenhouse studies show that it is an obligate annual. When it was first described, the morphological characteristics of the annual Stephanomerias were not known and, consequently, its relationships were obscured. It is now clear, however, that in morphological features, karyotype, and reproductive compatibilities, subspecies *carotifera* is closely allied to the other subspecies of *S. exigua*. For some of the characters that distinguish it from these subspecies, it varies toward *S. virgata* ssp. *virgata,* a situation that suggests the possible effects of past hybridization (Gottlieb, 1971).

The coastal and inland populations are alike in most of their morphological features but they can be separated by several characteristics of their pappus bristles. Inland populations have strongly thickened bristle bases whereas the bristles of the coastal populations are not or only very slightly thickened as described above. Reproductively, both are fully crossable, and their hybrids are highly fertile. The minor morphological differences and the full reproductive compatibility mean that there is neither taxonomic nor biological reason for distinguishing them. Populations of subspecies *carotifera* hybridize with both subspecies of *S. virgata* in northern Ventura County. A hybrid swarm is present where subspecies *carotifera* and subspecies *coronaria* meet at the junction of Roads G16 and G17 at the Arroyo Seco Bridge in Monterey County.

1d. **Stephanomeria exigua** ssp. **macrocarpa** n.ssp. Differt ab aliis subspeciebus capitulis in ramulis abbreviatis et tegulis valde reflexis, acheniis longioribus (5.5-6.8 mm longis).

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (5–10 mm) peduncles (fig. 2); heads averaging 6–8 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or white on upper surface, occasionally purple-tinged on back; achenes averaging 5.5–6.8 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 13–19 in number, often connate in five groups of 2–4 each, 6.2–7.5 mm long, plumose on the upper 60–70% of their length, strongly thickened and tawny at the base, remaining on the achene. **n = 8.**

Type. On Route 168, ½ mile east of Tollhouse on road to Pineridge, Fresno County, California, September 4, 1970, *Gottlieb 7048*. (Holotype: UC).

Distribution. On western slope of Sierra Nevada from 1000 to about 4000 feet from Kern County to Stanislaus County (fig. 1). Flowers August and September.

Representative specimens. CALIFORNIA. Kern Co.: 3–4 miles east of Glennville on Rt. 155, *G-7028*. Mariposa Co.: 8 miles southwest of Mariposa on Merced Road, *Stebbins 2653;* 1 mile south of east fork Chowchilla Bridge on Rt. 49, *G-6954*. Stanislaus Co.: Knights Ferry, *Eastwood July 25, 1923*. Tulare Co.: near Eleven

Range View Point, Sequoia National Park, *J. T. Howell 28901;* 12 miles south of Fountain Springs and approximately 7 miles north of California Hot Springs, *G-7042;* between Lemon Cove and Badger on J21, *G-7044.* Tuolumne Co.: 1½ miles northeast of Riverside Station on North Fork, Tuolumne River, *G-7052.*

Specimens of subspecies *macrocarpa* have rarely been collected although it is common within its limited range of distribution. The achenes of this subspecies are the largest of any of the annual Stephanomerias. Reproductively, it is close to subspecies *coronaria* and the two hybridize where they come together in Kern County. The strongly reflexed calyculate bracts of subspecies *macrocarpa* also relate it to subspecies *carotifera;* experimental hybrids between them have not yet been grown. Subspecies *macrocarpa* is self-compatible and it is highly self-pollinating in the greenhouse.

1e. **Stephanomeria exigua** ssp. **coronaria** (Greene) n. comb.
Stephanomeria coronaria Greene, Bull. Calif. Acad. 1:194. 1885.
Ptiloria coronaria Greene, Pittonia 2:132. 1885.
Stephanomeria exigua var. *coronaria* Jepson, Man. Fl. Pl. Calif. 998. 1925.

Herbage glabrous or sparsely pubescent on stems and involucres; head solitary or clustered on short (3–5 mm) peduncles (fig. 2); heads averaging 5–11 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white on upper surface, generally purple-tinged on back; achenes averaging 2.3–3.1 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 7–20 in number, plumose on the upper 60–85% of their length, thickened (at least slightly) and occasionally connate in groups of 2–4 at the bases, which often remain adnate to the achene. **n = 8.**

Type. "California, Santa Lucia Mountains, August, 1885. T. S. Brandegee." (Holotype: GH!)

Distribution (fig. 1). In California, widespread in many diverse habitats: equable maritime sites on off-shore islands and along coast from Goleta to Ventura; arid sandy soils in inner South Coast Ranges; raisin vineyards south of Fresno; openings in yellow pine forest to 6500 feet in Greenhorn and San Gabriel Mountains; volcanic soils in eastern Sierra Nevada to 9300 feet. In Oregon and Idaho on sandy or limestone or volcanic soils in sagebrush desert. Flowers July to October.

Representative specimens. CALIFORNIA. Contra Costa Co.: sand dunes at Antioch, near Kaiser plant, *G-6959.* Kern Co.: Tejon Pass, *J. T. Howell 27490;* Edison, *J. T. Howell 32702;* Castaic Valley, 1 mile south of Lebec on Frazier Park Road, *Twisselmann 8004;* entrance to Tehachapi Mountain Park, *G-7036;* 2.1 miles north of Greenhorn Summit on Tobias Pass Road, *G-7116;* ½ mile east of Woody on Route 155, *G-7117.* Inyo Co.: south side Wonoga Peak, *J. T. Howell, 26288;* Onion Valley Road, *J. T. Howell 27439;* 13.5 miles west of Bishop on Sabrina Lake Road, *G-6667.* Los Angeles Co.: Prairie Fork, San Gabriel River, *Johnston 1654;* ridge

southwest of Swartout Valley, San Gabriel Mountains, *Munz 7671;* Sepulveda Canyon, Santa Monica Mountains, *Raven and Thompson 14515;* ½ mile west of Tent Rock Campsite on West Liebre Lookout Road, *G-7054.* Mono Co.: Sherwin Grade, Rock Creek, Route 395, *Ferris 12584.* Monterey Co.: Limekiln Creek west of Gonzales, *Hoover 9973;* creek below Metz, *Twisselmann 9190.* San Bernardino Co.: Grass Valley Lake, *Raven and Beeks 16770.* San Luis Obispo Co.: 3 miles north of Pozo, *Hoover 9906.* Santa Barbara Co.: Goleta salt marsh, *Pollard, Oct. 10, 1957;* San Miguel Island, *Greene, September 1886.* Tulare Co.: Redstone Park, *K. Brandegee, July 25, 1905;* Bakeoven Meadows, *J. T. Howell 26936.* Ventura Co.: Pt. Mugu, *J. T. Howell 3139;* Mill Canyon, Lockwood Valley, *Twisselmann 17544;* Santa Cruz Island, ¼ mile east of Main Ranch, *Wolf 4168.* OREGON. Harney Co.: Malheur Lake, Narrows, *Henderson 8604.* NEVADA. Esmeralda Co.: 1.5 miles west of Lida, *Alexander and Kellogg 2386.* IDAHO. Owyhee Co.: ½ mile north of Oreana, *Davis 2072.*

Subspecies *coronaria* occupies the most diverse series of habitats of any annual *Stephanomeria.* Striking morphological variation is found within populations in terms of ligule number, size, and color. The number of pappus bristles and the proportion of the bristle that is plumose are both higher in populations in the South Coast Ranges than in populations in the Sierra and eastward. Moderate reductions in fertility are found in experimental hybrids between populations representing these two groups. In the southern Sierra Nevada and mountains of southwestern Nevada, subspecies *coronaria* is found from 5000 to 9300 feet and subspecies *exigua* at lower elevations. Where the two subspecies meet, intergrading individuals are often found.

2. Stephanomeria paniculata Nutt., Trans. Amer. Phil. Soc. 2: 7:428. 1841.

Ptiloria paniculata Greene, Pittonia 2:132. 1890.

Stephanomeria oregonensis Gandoger, Bull. Soc. Bot. Fr. 65:53. 1918. (Ochoco River, Oregon, *Cusick 2695*)

Stephanomeria suksdorfii Gandoger, loc. cit. (Bingen, Washington, *Suksdorf 5867*)

Herbage glabrous or occasionally short pubescent on stems and involucres; heads solitary or clustered on short (5–7 mm) peduncles (fig. 2); heads averaging five florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or white; achenes averaging 3.8–4.2 mm in length, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 15–18 in number, completely plumose to the base, generally connate in groups of 2–4 at the thickened, heavily setulose bases, usually remaining adnate to the achene. **n = 8.**

Type. "On the Rocky Mountain Plains, towards the Colorado", 1834–35, *T. Nuttall.* (Holotype: GH!)

Distribution (fig. 1). Open sandy or volcanic soils around Mt. Shasta and occasionally south to Plumas County, California. More common in eastern Oregon, Washington, and Idaho, often growing as a weed along

roadsides, particularly in the Columbia River gorge. Flowers June to August.

Representative specimens. CALIFORNIA. Plumas Co.: between Taylorsville and Genesee, *J. T. Howell 28209*. Siskiyou Co.: Mt. Shasta, *Grant 5064;* on U.S. 97, ¾ mile south of turnoff to Highway A12, north of Weed, *G-6682*. OREGON. Jefferson Co.: 2½ miles west of Metolius on road to Round Butte, *G-6686*. Sherman Co.: 6 miles west of Arlington on 8ON, *G-6691*. Wasco Co.: 2 miles west of The Dalles on U.S. 30, *G-6687*. WASHINGTON. Douglas Co.: Rock Island, *Sandberg and Leiberg 2303*. Klickitat Co.: Columbia River, *Suksdorf 982*. Walla Walla Co.: Waitsburg, *Horner 28*. Yakima Co.: 5 miles south of Toppenish on U.S. 97, *G-704*. IDAHO. Canyon Co.: Falks Store, *MacBride 1687*. Elmore Co.: King Hill, *Nelson and MacBride 1085*. Owyhee Co.: about 8 miles east of Silver City on road to Murphy, *G-719*.

Stephanomeria paniculata shows close phylogenetic affinities to *S. exigua* ssp. *coronaria*. It is self-compatible and is highly self-pollinating in the greenhouse. Correlated with its breeding system are short narrow ligules and reduced number of pollen grains.

3. **Stephanomeria diegensis** n. sp. Inter *S. exiguam* et *S. virgatam* quasi intermedia; ab *S. exigua* pappi setis non incrassatis, ab *S. virgata* acheniis sulcatis differt.

Heads solitary or clustered on short (3–4 mm) peduncles (fig. 2); heads averaging 11–13 florets; involucres subtended by reflexed calyculate bracts, glandular-puberulent; ligules various shades of pink or white on upper surface, generally purple-tinged on back; achenes averaging 1.9 to 2.3 mm long, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 19–21 in number; plumose on the upper 80–85% of their length, not thickened, distinct at the base, completely deciduous. **n = 8.**

Type. Near entrance to Torrey Pines State Park, San Diego County, California, August 15, 1966, *Gottlieb 66168*. (Holotype: UC)

Distribution (Gottlieb, 1971, fig. 3). Frequent in open, pioneer sites such as old clearings, the landward side of coastal sand dunes, chaparral openings, and sandy roadside embankments below 2000 feet from Santa Monica Mountains south to San Quintin, Baja California. Flowers August to November.

Representative specimens. CALIFORNIA. Los Angeles Co.: Santa Catalina Island, Descanso Canyon, *Millspaugh 4534;* canyon below Lemon Tank, San Clemente Island, *Raven 17978;* Mosquito Harbor, San Clemente Island, *Abrams and Wiggins 344;* Mandeville Canyon, Santa Monica Mountains, *Clokey and Templeton 4581;* U.S. 101, 0.2 miles east of Zuma Beach turnoff, Santa Monica Mountains, *Raven and Thompson 13721;* Inglewood, *Abrams 2979*. Orange Co.: Route 74 immediately west of Lower San Juan Campground, *G-6860*. San Diego Co.: La Jolla, *F. E. and E. S. Clements 269;* Del Mar, *Jepson 1607;* Coronado, *Spencer 1009;* Torrey Pines, *Raven and Wedberg 9474;* 4 miles north of Lakeside on Highway 67, *G-6637;* ¼ mile north of Rancho San Bernardo Road on U.S. 395, *G-66162;* 1½ miles west of Harbison Canyon Road on U.S. 8, *G-66164*. Ventura Co.: on Deer Creek Road, 2½

miles east of Route 1, *G-6945*. MEXICO. Baja California. 2 miles north of Rosario Beach, *Wiggins and Gillespie 3896;* San Quintin Bay, *Mason 2062a;* Middle Island, Coronado Islands, *Moran 6805;* South Cove, Todos Santos del Sur, *Philbrick and Benedict B68–421.*

The morphological characteristics of *Stephanomeria diegensis* are an amalgam of those of *S. exigua* and *S. virgata*. The evolutionary relationships of the species are fully described in Gottlieb, 1971.

4. Stephanomeria elata Nutt., J. Acad. Nat. Sci. Phil, n.s., 1.173, 1847.

Herbage glabrous or short pubescent or glandular-pubescent on branchlets and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 9–15 florets; involucres subtended by strongly reflexed, slightly reflexed, or rarely appressed calyculate bracts; ligules various shades of pink or white on upper surface, purple-tinged on back; achenes averaging 2.8–4.5 mm in length, five-sided with a narrow longitudinal groove on each side (fig. 3); pappus bristles averaging 17–22 in number, generally completely plumose (pinnae may be sparse in proximal 10% of bristle), the bases various, either not thickened, not connate, and completely deciduous, or thickened, connate in groups of 2–4, and remaining on the achene. **n = 16.**

Type. Holotype: "Santa Barbara, Upper California", not located at Phil. Acad. Nat. Sci. or British Museum. Neotype: Devereux Dunes, University of California, Santa Barbara Campus, Goleta, California, October 11, 1971, *Gottlieb and Philbrick 7140,* deposited at UC.

Distribution (fig. 4). Populations with thickened and connate pappus bristles are found in chaparral openings, grassy meadows, and along roadsides from Monterey County to southwestern Oregon in the Coast Ranges and also on the western slopes of the Sierra Nevada from 500 to 4500 feet south to Fresno County. Populations with unthickened and distinct bristles are distributed near the coast from Marin to Santa Barbara counties. Flowers from July to October.

Representative specimens. OREGON. Douglas Co.: 5 miles north of Jackson County line on Highway 227, *G-697*. Lane Co.: Willamette River near Oakgrove, *Henderson 16508*. CALIFORNIA. Amador Co.: 1.5 miles west southwest of Rich Gulch, *Belshaw 2478*. Alameda Co.: Strawberry Canyon, Berkeley, *Tracy 1953*. Eldorado Co.: 1 mile south of Coloma, *J. T. Howell 5575*. Humboldt Co.: White Thorn Valley, *Tracy 5034*. Lake Co.: 4 miles from Middleton on Adams Springs Road, *J. T. Howell 5449*. Marin Co.: south end Bolinas Ridge, Mt. Tamalpais, *J. T. Howell 21552;* on bluffs above ocean east of lighthouse, Point Reyes, *G-6958*. Mariposa Co.: 7 miles southwest of Mariposa on Merced Road, *Stebbins 2652*. Monterey Co.: headwaters of Arroyo Seco, *Mason 5745;* Laureles Grade, *G-66123*. Napa Co.: Wooden Valley Grade, *Raven 3057*. Nevada Co.: west of Greenhorn Creek, *Raven 7979*. San Francisco Co.: Lake Merced, *J. T. Howell 716*. San Luis Obispo Co.: mouth of Hazard Canyon, Morro Bay, *Chambers 2474;* Baywood Park, Santa Isabel Avenue, *G-66132*. San Mateo Co.: Pt. San Pedro, *J. T. Howell 15369*. Santa Clara Co.: Mt. Hamilton, *J. T. Howell 11718;* Skyline Blvd., 4 miles south of junction with Page Mill Road, *G-66120*. Santa Cruz Co.: head of San Lorenzo River,

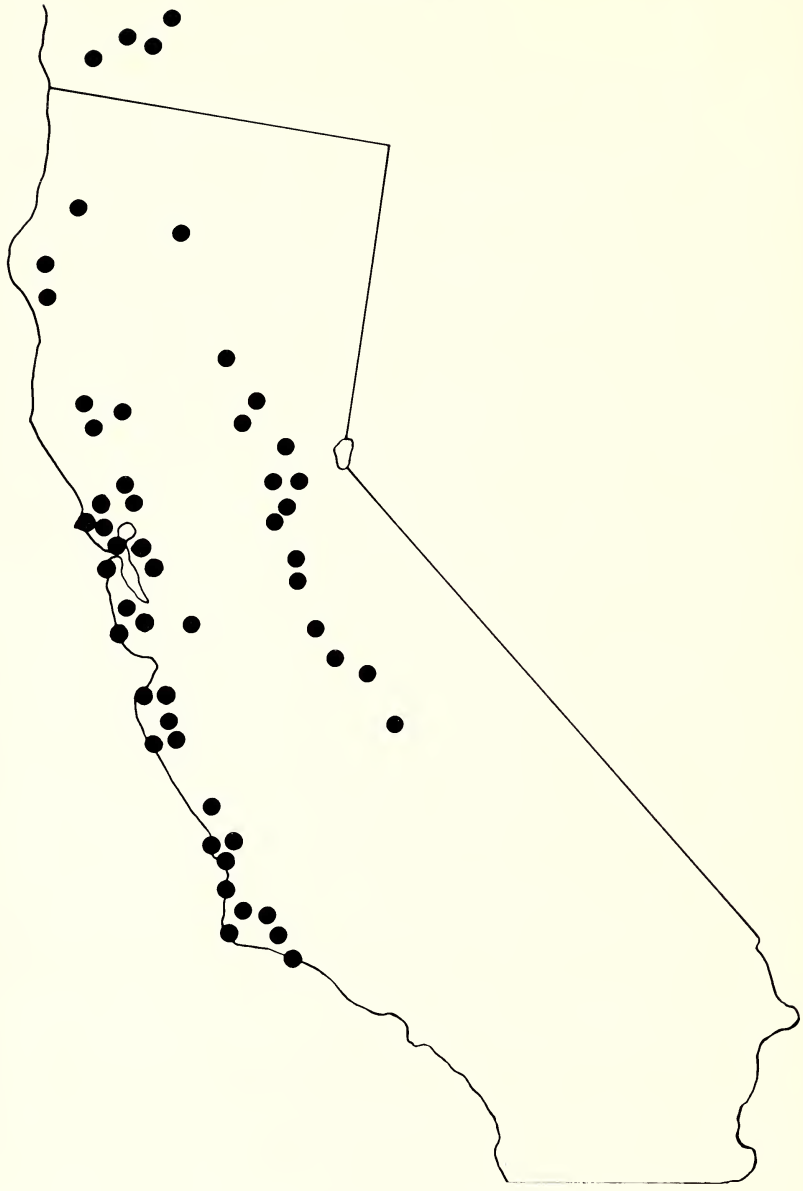

FIG. 4. Distribution of *Stephanomeria elata*.

Yates 4060. Sonoma Co.: Layton Mine, Austin Creek, *Hoffman 579*. Trinity Co.: Scott Mountain, 13.5 miles north of Carrville, *J. T. Howell 12831*. Yuba Co.: Camptonville, *J. T. Howell 28285*.

All the tetraploid populations of annual Stephanomerias are placed into *Stephanomeria elata.* These populations are self-compatible and are self-pollinating in the greenhouse. Substantial inter-population morphological variability is observed in the length, width, color, and number of florets and degree of reflexing of the calyculate bracts. In addition, two groups of populations can be distinguished on the basis of degree of thickening of the basal portion of the pappus bristles as described above. Populations with thickened bristles also have larger achenes, averaging 3.9–4.5 mm in length, whereas the achenes of populations without thickened bristles average 2.8–3.3 mm in length. Another difference is that 24–30% of the pollen grains of the former group of populations are tetracolpate. Where the two groups of populations overlap in Santa Cruz, Santa Clara, and Monterey counties, it is often difficult to assign individuals to one or the other. Because of their high degree of self-pollination, hybridization between the two groups has not yet been successful. Since the morphological differences are minor and intergrade individuals can be found, and since cytogenetic evidence (Gottlieb, 1969) suggests that the tetraploid populations are allotetraploid, by chromosomal doubling following interspecific hybridization between *S. exigua* and *S. virgata,* the tetraploid populations are placed in a single species.

Although I have been unable to locate the type specimen of *S. elata,* Nuttall's description is sufficiently clear in details of morphology that it is appropriate to apply this name to the tetraploid populations. No other name has ever been applied to tetraploid populations. Nuttall most likely described a small or depauperate specimen since he mentions that the specimen from which he drew his description had "a small terminal panicle". His statement that the flowers were "apparently blue" was probably based on the condition of the dried specimen; it is not unusual for ligules with strongly purple-tinged stripes on their lower surface to appear bluish when dry.

5a. STEPHANOMERIA VIRGATA Benth. ssp. VIRGATA, Bot. Sulph. 32. 1844.
Stephanomeria tomentosa Greene, Bull. Calif. Acad. 2:152. 1886. (Holotype: collected by E. L. Greene, Santa Cruz Island, July and August 1886, ND 001751! ND 001753! ND 001754!)
Ptiloria virgata Greene, Pittonia 2:130. 1890.
Stephanomeria virgata var. *tomentosa* Munz, Aliso 4:100. 1958.

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 8–9 florets; involucres subtended by strongly reflexed calyculate bracts; ligules various shades of pink or rarely white on upper surface, usually purple-tinged on back; achenes averaging 3.0–3.4 mm in length, five-sided with smooth or rugose but not grooved surfaces (fig. 3); pappus bristles averaging 23–28 in number, densely and completely plumose to the base, not thickened and distinct, completely deciduous. **n = 8.**

Type. San Pedro, Los Angeles County. (Holotype: Kew)

Distribution (Gottlieb, 1971, fig. 2). Chaparral openings and dry sandy hills in oak savanna from sea level to 6000 feet from southern San Luis Obispo to San Diego counties. Also abundant on roadsides and freeway embankments around Los Angeles. Flowers late July to October.

Representative specimens. CALIFORNIA. Los Angeles Co.: Mint Canyon Road 7 miles north of Solemint, *G-66155;* 1 mile south of Crystal Lake on Highway 39, *G-66157;* 4 miles south of Gorman on Gorman Post Road, *G-7055*. San Bernardino Co.: Cajon Pass, *Raven 16687;* Lytle Creek Road, ½ mile south of Applewhite junction, *G-66159*. San Luis Obispo Co.: between Suey Creek and Cuyama River, *Hoover 6480*. Santa Barbara Co.: ½ mile west of La Cumbre Lookout, *G-66148;* Point Sal Road, 1 mile west of Ranch, *G-6934*. Ventura Co.: 4 miles northeast of Devil's Heart Peak, *Simontacchi 137;* 2 miles south of Rose Valley Campground on Route 33, *G-66151*.

Historically, any annual *Stephanomeria* that had essentially fully plumose pappus was placed in this species. Now it is known that fully plumose pappus bristles are a feature of many of the taxa. *Stephanomeria tomentosa* refers to a tomentose form originally thought to be restricted to the California offshore islands; it has now been commonly found in many populations.

5b. **Stephanomeria virgata** ssp. **pleurocarpa** (Greene) n. comb.

Ptiloria pleurocarpa Greene, Pittonia 2:131. 1890.

Ptiloria canescens Greene, Pittonia 2:131. 1890. (Paratype: collected by E. L. Greene, Alameda, June, 1890. ND 001745!)

Stephanomeria virgata var. *pleurocarpa* Hall, Univ. Calif., Publ. Bot. 3:258. 1907.

Herbage glabrous or tomentose on stems and involucres; heads solitary or clustered on short (3–7 mm) peduncles (fig. 2); heads averaging 5–6 florets; involucres subtended by appressed calyculate bracts; ligules various shades of pink or rarely white, occasionally purple-tinged on back; achenes averaging 2.2–3.6 mm in length, five-sided with smooth or rugose but not grooved surfaces (fig. 3); pappus bristles averaging 23–28 in number, densely and completely plumose to the base, not thickened and distinct, completely deciduous. $\mathbf{n = 8}$.

Type. Redding, Shasta County, collected by E. L. Greene, 1889. (Holotype: ND 001621!)

Distribution (Gottlieb, 1971, fig. 2). Many soil types including shale, sandstone, serpentine, and volcanics. Widely distributed from southwestern Oregon in the Coast Ranges and Sierra Nevada (below 6000 feet) to northern Baja California. Also occasional populations in mountains of north central Nevada. Flowers July to November.

Representative specimens. OREGON. Curry Co.: mouth of Fall Creek on Illinois River, *Baker 4877*. Douglas Co.: 3 miles north of Drew on 227, *G-696*. Jackson Co.:

Elk Creek, Rogue River, *Henderson 13082*. NEVADA. Washoe Co.: Incline Road, Lake Tahoe, *Kennedy 1474*. CALIFORNIA. Alameda Co.: Redwood Ridge *Constance 421*. Amador Co.: 2 miles south southwest of Volcano, *Johannsen 21505*. Calaveras Co.: Big Trees, *Howden 12670*. Contra Costa Co.: Marsh Creek, 6 miles east of Clayton, *Rose 38308*. Fresno Co.: Hume Lake, *J. T. Howell 16150*. Humboldt Co.: Trinity River, near mouth of Willow Creek, *Tracy 5187*. Kern Co.: 7 miles west of Maricopa, *Twisselmann 1604*. Lake Co.: 1 mile below Hullville on Eel River, *Heller 6021;* southwest side of Snow Mountain, 5000 feet, *Stebbins 2066;* Bartlett Springs Road, north of Lucerns, *G-6699*. Mariposa Co.: Wawona, *J. T. Howell 583*. Mendocino Co.: Mendocino, *Brown 900*. Monterey Co.: along San Antonio River between Jolon and Santa Lucia Ranger Station, *Mason 5788;* 9 miles north of Parkfield on Road to 198, *G-7081*. Napa Co.: 1.3 miles east of Chiles Valley, *Raven 3950;* Mt. St. Helena, *Eastwood, 7956*. Plumas Co.: Sierraville, *Hanks 6566*. Riverside Co.: Chalk Hill, San Jacinto Mountains, *Hall 2631*. San Benito Co.: 4 miles north of The Pinnacles, *J. T. Howell 11538*. San Diego Co.: immediately south of boundary Cuyamaca State Park, Route 79, *G-6866*. San Luis Obispo Co.: between Rocky Butte and Pine Mountain, *Hoover 8399*. Shasta Co.: Burney Falls, *Rose 45222*. Sutter Co.: 4 miles south of Live Oak, *Heller 13834*. Tulare Co.: Paradise Creek, *Frost 7895*. Tuolumne Co.: Mather, *Mason 2176*.

Populations of this subspecies are occasionally sympatric with populations of *S. exigua* and subspecies *virgata*. Hybrid individuals have been found in all such contact zones. *Ptiloria canescens* refers to a pubescent form that is a genetic variant and one commonly found in many populations throughout the distribution.

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